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**Species roles in plant-pollinator communities are conserved across native
and alien ranges**

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21 **ABSTRACT**

22 *Aim.* Alien species alter interaction networks by disrupting existing interactions, for example
23 between plants and pollinators, and by engaging in new interactions. Predicting the effects
24 of an incoming invader can be difficult, although recent work suggests species roles in
25 interaction networks may be conserved across locations. We test whether species roles in
26 plant-pollinator networks differ between their native and alien ranges, and whether the
27 former can be used to predict the latter.

28 *Location:* worldwide.

29 *Methods.* We used 64 plant-pollinator networks to search for species occurring in at
30 least one network in its native range and one network in its alien range. We found 17
31 species meeting these criteria, distributed in 48 plant-pollinator networks. We characterized
32 each species' role by estimating species-level network indices: normalised degree, closeness
33 centrality, betweenness centrality, and two measures of contribution to modularity (c and z
34 scores). Linear Mixed Models and Linear Regression Models were used to test for
35 differences in species role between native and alien ranges and to predict those roles from
36 the native to the alien range, respectively.

37 *Results.* Species roles varied considerably across species. Nevertheless, although species
38 lost their native mutualists and gained novel interactions in the alien community, their role
39 did not differ significantly between ranges. Consequently, closeness centrality and
40 normalised degree in the alien range were highly predictable from the native range
41 networks.

42 *Main conclusions.* Species with high degree and centrality define the core of nested
43 networks. Our results suggest that core species are likely to establish interactions and be
44 core species in the alien range, whilst species with few interactions in their native range will
45 behave similarly in their alien range. Our results provide new insights into species role
46 conservatism, and could help ecologists to predict alien species impact at the community
47 level.

48 **Key-words:** biological invasions, centrality, conservatism, ecological networks, pollination,
49 predicting invasion

50 INTRODUCTION

51 Predicting novel species interactions is a crucial challenge in today's rapidly changing world.
52 Alien species are an important driver of novel ecosystems (Hobbs *et al.*, 2006) due to their
53 ability to outcompete native species (Chittka & Schurkens, 2001; Madjidian *et al.*, 2008; Roy
54 *et al.*, 2012), change the community structure (Albrecht & Gotelli, 2001; Memmott & Waser,
55 2002; Carpintero *et al.*, 2005) and disrupt species interactions (Aizen *et al.*, 2008; Traveset &
56 Richardson, 2006; Tylianakis *et al.*, 2008). Studies on alien species mostly focus on species
57 considered to be invasive, which means that rather little is known about those alien species
58 that remain at low population size or have fewer interactions with (and hence, impact on)
59 the recipient community.

60 While many studies have tried to identify key features that predict which species will
61 become invasive and which communities are more likely to be invaded (Thuiller *et al.*, 2005;
62 Richardson & Pysek, 2006; Pysek & Richardson, 2007) these remain of limited practical
63 value. For example it remains difficult to predict whether a mutualistic interaction will
64 facilitate the establishment and dispersal of an alien species (Hulme, 2012). The limited
65 practical value of current work is partially due to the need for detailed information on each
66 species involved in the potential novel interactions, which is usually very time consuming to
67 gather. Therefore, new methods to simplify predictions are required. An alternative could
68 be to assess the role a given species plays in the topology of interaction networks (e.g.
69 Stouffer *et al.* 2012; Martin Gonzalez *et al.*, 2010; Albrecht *et al.* 2014). Species roles
70 summarize their ability to interact with, and potentially affect, other species in the
71 community in a way that is relatively easy to sample compared with measures of multiple

species and community traits. The application of species roles in ecological networks to predict invasion currently remains untested.

Ecological networks have been of considerable use when trying to understand how alien species integrate into local communities (Memmott & Waser, 2002; Garcia *et al.*, 2014, Maruyama *et al.*, 2016) and how they affect the overall mutualistic network structure (Olesen *et al.*, 2002a; Santos *et al.*, 2012; Albrecht *et al.*, 2014). In general, alien species are generalists, i.e. they interact with many species in the community in which they occur (Aizen *et al.*, 2008; Santos *et al.*, 2012). Generalist species tend to occupy central positions in ecological networks, and by interacting with other generalists and specialists (Memmott & Waser, 2002; Aizen *et al.*, 2008) they contribute to the pattern of nestedness that characterises many mutualistic networks (Bascompte, 2003; Bascompte & Jordano, 2007). In addition to its number of direct interaction partners (termed 'degree'), a species' position allows it to connect different parts of the network and maintain network cohesiveness. This helps to define its role in structuring the overall network topology (Martin Gonzalez *et al.*, 2010), including elements of network structure such as clustering or modularity (Olesen *et al.*, 2007). Thus, the species' position in the network, i.e. its network role, captures key information on its interactions with, and potential effects on, other species in the community.

Recent work suggests that species roles are conserved across different locations. Species interactions, either generalist or specialist, have been shown to be phylogenetically conserved across space and time (Jordano *et al.*, 2003; Rezende *et al.*, 2007; Gómez *et al.*, 2010), because intrinsic (inherited) characteristics of species can constrain who can interact with whom (Eklöf *et al.*, 2013) and can be related to native and alien species roles in

95 network topology (Maruyama *et al.*, 2016). If these traits show low intraspecific variability
96 across locations, this indicates that species roles in networks should also be conserved. For
97 example, species roles in predator-prey networks can be conserved from an evolutionary
98 perspective, such that dynamically-important species in one network will be important in
99 the other networks in which it occurs (Stouffer *et al.*, 2012). Similarly, species roles in host-
100 parasitoid networks were found to be intrinsic characteristics conserved over different
101 temporal and spatial scales (Baker *et al.*, 2015).

102 Despite evidence of an intrinsic component of species network roles, species
103 interactions and network roles may also be affected by local environmental and biotic
104 conditions (Tylianakis *et al.*, 2008; Trøjelsgaard *et al.*, 2015). Moreover, the number and
105 type of interactions a species has increase with that species' abundance (e.g., Trøjelsgaard
106 *et al.*, 2015), and species abundance and interactions may change during different stages of
107 invasion (Aizen *et al.*, 2008). Finally, patterns of non-random association among species
108 based on their phylogenetic relatedness (Rezende *et al.*, 2007) suggest that coevolved
109 interactions may be important for structuring mutualistic networks. Therefore, it is currently
110 not clear whether species roles can be extrapolated from one location to another that
111 differs in its evolutionary history and local community traits.

112 Here we aim to understand whether species roles differ and can be predicted from
113 the native to the alien range of their distribution. Specifically, we use measures of plant and
114 insect species roles in plant-pollinator networks (normalised degree, closeness and
115 betweenness centrality, and *c* and *z* scores) recorded in both their native and alien ranges to
116 test whether they differ consistently or can be predicted between ranges. Based on the
117 findings that species roles and ecological interactions can be temporally, spatially and

phylogenetically conserved (Rezende *et al.*, 2007; Gómez *et al.*, 2010; Stouffer *et al.*, 2012; Baker *et al.*, 2015) we predict that a species' network role will be similar in its native and alien ranges, such that the former can be used to predict the latter. By including both specialist and generalist species we can draw conclusions about both rare and common alien species.

METHODS

We searched for plant-pollinator networks where we could potentially find species recorded in both their native and alien range. We found 48 plant-pollinator networks of which 42 were downloaded from the "Web of Life" database (Ortega, 2014), three are our own data sampled in New Zealand and three are unpublished data from Lopezaraiza-Mikel and Memmott in Hawaii; Table S1). Our criteria of species/network inclusion in the dataset was to have a target species occurring in at least one network as native and one network as alien. Thus each network can contain more than one target species, each of which may be either in its native or its alien range. As some of these networks contain only the presence/absence of interactions and the sampling effort of these networks is mostly unknown, we analysed all networks as binary matrices. In addition, here a flower visitor was considered to be a pollinator, irrespective of whether effective pollination was demonstrated. To define species range as native or alien, we used the following online information: Global Invasive Species Database (<http://www.issg.org/database/welcome/>), Global Invasive Species Information Network (<http://www.gisin.org>), Delivering Alien

140 Invasive Species Inventories for Europe (<http://www.europe-aliens.org/>), GB Non-Native
141 Species Secretariat Website (<http://www.nonnativespecies.org>), Plant Pest Information
142 Network of New Zealand (<http://archive.mpi.govt.nz/applications/ppin>), Centre for Invasive
143 Species and Ecosystem Health (<http://www.bugwood.org/>), Weeds in Australia
144 (<http://www.environment.gov.au/biodiversity/invasive/weeds/>), and Invasive Species of
145 Japan (<https://www.nies.go.jp>).

146

147 **Species roles**

148 Species roles in networks can be described by a variety of different, yet often correlated
149 metrics. Our intent here was not to provide an exhaustive comparison of different potential
150 measures of species roles, or to determine which metrics were best conserved and why.
151 Rather, we focused on testing a ‘proof of concept’ that roles could be conserved, so we
152 focused on five complementary metrics that could potentially capture different aspects of
153 species ecology:

154 1) Normalised degree – the number of interactions per species (i.e. degree) divided
155 by the number of possible interacting partners, which controls for differences in network
156 size. Normalised degree is the most local centrality index that characterizes a species’
157 network position, such that species with high degree are core in the network structure and
158 enhance robustness (Solé & Montoya, 2001; Dunne *et al.*, 2002). Additionally, normalised
159 degree estimates how generalist/specialist a species is relative to other species in the same
160 trophic level of the community in which it occurs.

2) Closeness centrality (hereafter, closeness) – the average distance (path length) to all other species in the network. Closeness incorporates the number of immediate connections to adjacent nodes and the connections of those nodes, so is a more global measure of location than degree. In bipartite networks, closeness and betweenness are measured for the unipartite projection of each trophic level based on shared interaction partners, such that higher closeness indicates a greater number of interaction partners shared with other species in the same trophic level that also share partners with many other species (Freeman, 1979; Martín Gonzalez *et al.*, 2010). Thus, closeness is a measure of niche overlap with other species at the same trophic level via shared pollinators and the potential for either positive or negative indirect effects via short path lengths (Morales & Traveset, 2008; Carvalheiro *et al.*, 2014).

3) Betweenness centrality (hereafter, betweenness) – the proportion of the shortest paths linking any pair of species in the network that cross through a given species. It estimates species importance for network cohesiveness (Freeman, 1979; Martín Gonzalez *et al.*, 2010). Species with high betweenness can potentially connect different parts of the network that could be otherwise sparsely linked or even isolated; thus alien species that tend to be highly generalist may be linking previously isolated species in plant-pollinator networks and affect the overall network structure.

4) and 5) *c* and *z* scores: the combination of these two metrics describes a species' role in the topology of the network as a hub, peripheral or connector within and among modules (Olesen *et al.*, 2007) based on the modularity of the network (Guimera & Amaral, 2005). The *z*-score calculates the standardized number of links a species has within a module, and the *c*-score calculates the among module connectivity, which is the number of

links a given species establishes among different modules. Therefore, high values of c and z are related to generalist species that have many interactions throughout the whole network, either as hubs connecting species within modules, or as connectors linking different modules. On the other hand, low values of c and z describe peripheral species that tend to be specialists. Alien plant species that invade a new range may act as network hubs by attracting many different pollinator species through providing high amounts of nectar, for example, Himalayan balsam (*Impatiens glandulifera* Royle) acts as a “magnet species” in its alien range (Chittka & Schurkens, 2001, Lopezaiza-Mikel et al. 2007), whilst alien pollinator species may act as network connectors while searching for floral resources in different modules.

To allow comparisons across networks with different size, closeness and betweenness were each scaled to sum to 1. Species role metrics were calculated using bipartite (Dormann *et al.*, 2009) and rnetcarto packages (Doulcier, 2015) for R; correlations among these metrics are shown in Table S5.

Statistical analysis

Are there differences in species roles in their native vs. alien range?

To answer whether species roles differed from native to alien ranges we used Linear Mixed-Effects Models (LMMs) in the lme4 package (Bates *et al.*, 2014). Individual models were fitted for normalised degree, closeness, betweenness, and c - and z -scores. The first four metrics were logit transformed to solve the issue of being bounded from zero to one (Warton & Hui, 2011). Range (native vs. alien) was modelled as a fixed factor, whilst

network and species were fitted as random effects to account for multiple observations from the same network and to group native and alien measures from the same species. Residual plots were used to check model adherence to assumptions. The overall variance explained by the model, and the proportion that could be attributed to the fixed factor (range) and the random factors were estimated by calculating: i) conditional Pseudo R-squared ($R^2_{GLMM_{(fix+rand)}}$), to estimate total variance explained by the fixed and random effects combined, ii) marginal Pseudo R-squared ($R^2_{GLMM_{(fix)}}$), to estimate the variance explained by range, and iii) the difference between the two ($R^2_{GLMM_{(fix+rand)}} - R^2_{GLMM_{(fix)}}$) to estimate the contribution of the random effects only ($R^2_{GLMM_{(rand)}}$) (Nakagawa & Schielzeth, 2013), using the MuMIn package (Barton, 2013). Then, to determine if any difference in species roles between native and exotic range could have occurred due to biogeographical patterns from tropical to temperate zones (Olesen & Jordano, 2002; Schleuning *et al.*, 2012), we re-ran the above models including the absolute latitude as a fixed effect interacting with range. Likewise, we re-ran the models with trophic level (plant or pollinator) and its interaction with range to determine whether any differences between native and alien range only applied to one trophic level.

Does a species' role in the native range predict its role in the alien range?

To test whether a species' role in the native range can predict its role in the alien range, we fitted five linear regressions relating species' mean normalised degree, closeness, betweenness, and the *c*- and *z*-scores in the alien range to the mean values in their native range. Normalised degree was strongly influenced by an outlier, which was removed and consequently improved model fit (Appendix S1). Model validation to check for

229 homoscedasticity and normality of the residuals was performed following Crawley (2013)
230 and Zuur et al. (2009). As previously, we re-ran these regressions including, separately,
231 absolute latitude and trophic level and their interactions with species' role in the native
232 range to determine whether the predictive power depended on these variables. Latitude
233 was determined for each species as the absolute difference between latitudinal mean in the
234 native range and the latitudinal mean in the alien range. The latitudinal mean was obtained
235 by averaging the absolute latitude of all occurrences each species has in its native and alien
236 ranges.

237 Subsequently, we jack-knifed the linear regression models to provide an unbiased
238 assessment of how accurately species roles could be predicted in alien networks based on
239 their mean role in the native networks (Efron, 1983). Each species was removed from the
240 linear regression in turn, the regression re-fitted, and predictions of the role metrics were
241 generated for that species in the alien networks based on its mean value across its native
242 networks. The observed mean values in the alien range were then compared against the
243 predicted values using Pearson's correlations. Individual species roles and mean species
244 roles were tested for correlation (presented as the Spearman coefficient in Table S5) and a
245 Bonferroni correction was used in both LMMs and LMs. All statistical and network analyses
246 were run in R v. 2.15.3 and v. 3.1.1 (R Core Team, 2014).

247

248

249 **RESULTS**

250 We compiled information on 12 plant species and five pollinator species that occurred in at
251 least one network in a native range and one network in an alien range (Table 1). These 17
252 species, from 19 different countries, were distributed in all continents except Antarctica
253 (Fig. 1, Table S1); this translates into a large range of different habitats, climatic conditions
254 and species richness. In total, we worked with 167 occurrences of the 17 target species (i.e.
255 one occurrence corresponds to the occurrence of a species in either its native or alien
256 range; note that multiple target species can occur in the same network) (Table S2).

257

258 **Are there differences in species roles in their native and alien range?**

259 There was no significant difference between native and alien ranges in any of the measures
260 of species' role (Table 2). In other words we found no evidence that, for example, species
261 consistently interact in a more generalist way in their exotic vs. native range. Rather, the
262 variance explained by the models was primarily attributable to the random factors
263 ($R^2_{\text{GLMM}(\text{rand})}$ was 94%, 40%, and 20% in the closeness, normalised degree and
264 betweenness models respectively), which were the network and the species identity, whilst
265 range, the fixed term, was not statistically significant for any of the metrics tested (Table 2).
266 Similarly, the random structure explained around one third of the variance in the z-score
267 (29%) and the c-score models (37%). The large variance retained by the random structure
268 suggests that species differ considerably in their network roles and that, unsurprisingly,
269 species roles depend on the local network (e.g., network size constrains the range of
270 possible roles), and this large variance within native or exotic ranges of a species blurred any
271 significant differences between them.

Even though network architecture can change across regions (Olesen & Jordano, 2002), we found no systematic change in species roles with latitude, neither significant range x latitude interaction (Table S3). However, a significant range x trophic level interaction for closeness (Table S3) revealed that the native range had lower closeness for pollinators but not for plants. This indicates that pollinators may move into a more central role in their alien range by pollinating generalist plants that are also pollinated by many other species and share those pollinators with many other plants. Given that in our analyses there were more plant species than pollinator species, this interaction effect captured the difference between ranges for pollinators that was otherwise masked by the lack of difference on plant species. Moreover, pollinator species had higher *c*-scores than plant species independently of range, suggesting that the pollinators included in our analyses may be better network connectors (Table S3). In fact, most plant and pollinator species played peripheral roles in our networks (73%) but pollinators were the main connectors (88%), module hubs (75%) and the only network hubs (100%) (Table S4).

Does a species' role in the native range predict its role in the alien range?

Two measures of species roles, closeness and normalised degree, in the alien range could be predicted from the native range data ($F_{1,15} = 27.32$, $p = 0.0001$, $r^2 = 0.62$ and $F_{1,14} = 13.56$, $p = 0.0025$, $r^2 = 0.46$, respectively; Fig. 2). The coefficients for closeness and normalised degree were 0.98 ($SE \pm 0.187$) and 0.71 ($SE \pm 0.192$), respectively, and both had intercepts that did not differ significantly from zero (closeness: $t = 0.25$, $p = 0.809$; normalised degree: $t = 0.67$, $p = 0.512$), suggesting that a species' role in the native range is associated to that in the alien range. In contrast, the positive trend in the relationship between native and alien

range when estimating betweenness (slope = $0.208 \text{ SE} \pm 0.109$) and the z-score (slope = 0.412 ± 0.204) was marginally non-significant ($F_{1,15} = 3.63$, $p = 0.076$, $r^2 = 0.14$ and $F_{1,15} = 4.07$, $p = 0.062$, $r^2 = 0.16$, respectively; Fig. 2) and lacked any significance for the c-score model ($F_{1,15} = 0.22$, $p = 0.649$). Although the testing of correlated variables (Table S5) increases the probability of type I error, the effects for closeness and normalised degree remained significant when a Bonferroni correction was applied (corrected alpha = 0.01). Moreover, out of five variables tested, the probability of finding two significant at an alpha below 0.0025 is extremely low (6.2×10^{-5} , calculated using the Bernoulli process described in Moran 2003), indicating that overall the suite of species roles in the exotic range could be predicted better from roles in the native range than would be expected by chance.

The predictive effects of closeness and normalised degree were consistent when latitude and trophic level were included in the models (Table S4). Neither latitude (normalised degree: $F_{3,13} = 0.355$, $p = 0.787$; closeness: $F_{3,13} = 1.61$, $p = 0.235$; betweenness: $F_{3,13} = 0.938$, $p = 0.450$; c-score: $F_{3,14} = 2.00$, $p = 0.173$; z-score: $F_{3,14} = 0.56$, $p = 0.652$) or trophic level (normalised degree: $F_{3,13} = 0.262$, $p = 0.851$; closeness: $F_{3,13} = 1.708$, $p = 0.214$; betweenness: $F_{3,13} = 1.044$, $p = 0.406$; c-score: $F_{3,14} = 2.00$, $p = 0.173$; z-score: $F_{3,14} = 0.56$, $p = 0.652$) showed any significant interaction with range when tested for predictive effects of species roles from the native to the alien range of a species distribution (Table S4). Congruent with the LMM results, after model selection we detected that the mean c-score was also higher for pollinators than for plants independently of range ($F_{2,14} = 12.02$, $p = 0.0009$).

In the jack-knife validation of our predictions, predicted values of closeness in the alien range were highly correlated with the corresponding observed values ($t = 15.339$, $p <$

0.0001, $r = 0.777$), suggesting that the species closeness in the native range is a good predictor of the species closeness in the alien range. The predictive power of native range was lower but still a good predictor for more than half of the species when estimating normalised degree ($t = 9.040$, $p < 0.0001$, $r = 0.583$), z-score ($t = 8.0445$, $p < 0.0001$, $r = 0.53$), and c-score ($t = 8.587$, $p < 0.001$, $r = 0.56$), though not as good for betweenness ($t = 5.621$, $p < 0.0001$, $r = 0.401$).

DISCUSSION

Two consistent patterns emerged from our analyses of the 48 datasets: 1) although species differed considerably in their roles, the roles of species generally did not differ consistently between their alien and native ranges, and 2) two metrics of species roles, closeness and normalised degree, in the alien range could be predicted from the native range. Betweenness and z-score predictions from the native to the alien range were marginally non-significant, but showed a trend toward positive correlation, which was unsurprising in the case of betweenness, given its high correlation with normalised degree and closeness (Table S5b). Despite this overall predictive ability, we found that pollinators (but not plants) had a higher closeness in their alien range, probably due to their ability to exploit a wide range of resources and thus interact with generalist plants. Still, trophic level (pollinator vs. plants) did not interact significantly with range, except for c-score, which showed higher values for pollinators, suggesting they may play a better role in connecting the whole networks than did plants. Our results suggest that species role conservatism may occur,

such that species that are generalists or play a central role in their native network are likely to play a similar role in their alien range.

Limitations

In an ideal situation, the networks studied would have been collected using the same methods, aiming for quantitative data collected over similar periods of time. The dataset used comes from different sources that used different sampling methodologies, spatial and temporal scales. Moreover, it contains only species that successfully established in the alien range thus it lacks information for those species that failed to establish in the alien range. Moreover, our models do not consider species abundance, which is known to drive some network patterns (Blüthgen *et al.*, 2007; Dorado *et al.*, 2011; Staniczenko *et al.*, 2013; Fort *et al.*, 2016) as well as the effects of invasive species (Dostal *et al.*, 2013; Carvalheiro *et al.*, 2014; Traveset & Richardson, 2014). Furthermore, the conservation status of the areas from which the networks were sampled is mostly unknown. Thus, the native range should not be necessarily interpreted as a pristine environment given that we are likely working with altered environments in both ranges. This high heterogeneity in the dataset generated high variance across different networks (even within a species' native or alien range), which would have reduced the probability of detecting differences across 'treatments'. In that sense, the absence of evidence for differences in species roles in native vs. alien range cannot be viewed as evidence of absence. That said, the positive correlations we observed between native- and alien-range values of closeness and normalised degree were robust enough to be seen despite the data being averaged across these heterogeneous replicate networks and spanning species with a range of roles from specialists to generalists.

364 **The intrinsic roles of alien species in pollination networks**

365 The correlation between species roles in their native and alien range in the five network
366 statistics concurs with other authors who report that species have intrinsic properties in
367 ecological networks that persist over temporal and spatial scales (Jordano *et al.*, 2003;
368 Gómez *et al.*, 2010; Stouffer *et al.*, 2012; Baker *et al.*, 2015). From the roles estimated here,
369 high degree and high closeness define the core of the nested network (i.e. those generalists
370 that interact with both specialists and generalists), and our results suggest that core species
371 will tend to maintain this role even when they enter novel communities. Species with high
372 degree, i.e. generalists, are expected to be good invaders because they can increase their
373 chance to establish and spread through the population by interacting with many of the
374 “available” species. Conversely, specialist species with few interactions in the native range
375 will also have only few interactions in the alien range, and this may lower their chance of
376 establishing into the novel community if, for example, the resource is scarce and
377 competition strong (Aizen *et al.*, 2008; Aizen *et al.*, 2012), as shown in previous work that
378 simulated invasion of food webs (Romanuk *et al.*, 2009). In turn, high closeness can be seen
379 in species that interact with other central species in the community, even if the focal species
380 is not a generalist itself. In fact, in our dataset the average normalised degree and average
381 closeness were not significantly correlated ($r = 0.24$, Table S5b), such that a species could
382 occupy a consistently central position in networks by interacting with central species, rather
383 than by being a generalist itself. Therefore, the combination of degree and closeness can
384 potentially be good indicators of species with high risk of introduction success in terms of
385 invasion. On the other hand, the poor prediction of betweenness and the c - and z -score,

which indicate the role a species plays as connecting different parts of the network, suggests that the role of species as connectors may depend on the distribution of species into modules.

Most plant species depend on animal species for pollination (Waser & Ollerton, 2006; Ollerton *et al.*, 2011), thereby any characteristic that enhances interactions with pollinators would likely be favourable when colonizing a new area. Central alien plants may have an advantage in the new range in terms of gene flow if local pollinators show high fidelity. A greater number of pollinator species constantly visiting different conspecific flowers may promote greater deposition of conspecific pollen grains, therefore increasing pollination (Brosi & Briggs 2013; Huang *et al.*, 2015). Nevertheless, the benefits of this increased visitation frequency may be partly offset by an increase in heterospecific pollen transport (Fang & Huang 2013) if, instead, the alien plant interacts with a generalist pollinator that visits different plant species therefore increasing heterospecific pollen transfer, potentially reducing seed set (Ashman & Arceo-Gómez, 2013). Still, heterospecific pollen transfer has been shown to be generally low and have none, low or species-specific effect on plant reproduction (Bartomeus *et al.*, 2008; Montgomery & Rathcke, 2012; Fang & Huang, 2013; Emer *et al.*, 2015). Moreover, central pollinator species may have an advantage over less connected species when arriving in an alien community due to their ability to visit different flower species, thereby obtaining different food resources (Traveset *et al.*, 2013). Pollinators were the main connectors in our networks and that was more frequent in their alien range. Given that the main pollinator connectors in our network were social insects (i.e. *Apis mellifera* and *Bombus* spp.), which are usually highly abundant in invaded areas (e.g. Aizen *et al.*, 2008; Santos *et al.*, 2012), and whose foraging individuals

reflect the colony needs (Willmer & Finlayson 2014 and references therein), it may be that these species' roles vary according to their population density and foraging behaviour. Yet, central pollinator species may face high competition with the local pollinators with which they share interactions, a constraint that may make it difficult for pollinators to establish in a novel community with low nectar/pollen resources, for example.

Our findings also have implications for network persistence. Rewiring, i.e. the reshuffling of interaction links among species, can enhance network resilience and robustness to disturbance (Staniczenko *et al.*, 2010; Kaiser-Bunbury *et al.*, 2011; Olesen *et al.*, 2011). Given that both plant and pollinator links can be transferred from native generalist to alien generalist species (Aizen *et al.*, 2008), and that the probability of a native pollinator interacting with an alien plant increases with its degree and nestedness contribution (Stouffer *et al.*, 2014), the introduction of a highly generalist alien species may affect not only the local generalist species but also the more specialized ones that connect to it via interaction rewiring (Aizen *et al.*, 2008). The consequences of this will depend on the centrality of the introduced species in combination with that of the native species, e.g. highly-connected alien species will likely promote local species rewiring, whilst the arrival of a poorly-connected species (i.e. a specialist) may have a mild or even neutral effect on local species interactions. Moreover, a species that remains in its home range in which the community has changed due to local extinctions and alien species invasion will find itself in a novel network of interactions. Given that species roles are conserved, rewiring of interactions will be needed for the local species to fit into the novel community (Gilljam *et al.*, 2015).

Conclusions

In summary, there seems to be an intrinsic component of species roles in plant-pollinator networks that is conserved across species native and alien ranges. Our results suggest that the core network position that a species occupies when introduced in a novel community will resemble how generalist or specialist it is in its native community. Our results provide new insights into the recent literature about interactions and species role conservatism, and have implications regarding the potential links that alien species may be able to create or disrupt once introduced into novel communities. Further studies incorporating community traits and the phylogenetic relationship between species with species network roles will advance our understanding of how alien species interact with, and potentially drive the formation of, novel communities.

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454

455 REFERENCES

456 Aizen, M.A., Morales, C.L. & Morales, J.M. (2008) Invasive mutualists erode native
457 pollination webs. *Plos Biology*, **6**, 396-403.

458 Aizen, M.A., Sabatino, M. & Tylianakis, J.M. (2012) Specialization and rarity predict
459 nonrandom loss of interactions from mutualist networks. *Science*, **335**, 1486-1489.

460 Albrecht, M. & Gotelli, N.J. (2001) Spatial and temporal niche partitioning in grassland ants.
461 *Oecologia*, **126**, 134-141.

462 Albrecht, M., Padrón, B., Bartomeus, I. & Traveset, A. (2014) Consequences of plant
463 invasions on compartmentalization and species' roles in plant-pollinator networks.
464 *Proceedings of the Royal Society B-Biological Sciences*, **281**, 20140773.

465 Ashman, T.L. & Arceo-Gómez, G. (2013) Toward a predictive understanding of the fitness
466 costs of heterospecific pollen receipt and its importance in co-flowering
467 communities. *American Journal of Botany*, **100**, 1061-1070.

468 Baker, N.J., Kaartinen, R., Roslin, T. & Stouffer, D.B. (2015) Species' roles in food webs show
469 fidelity across a highly variable oak forest. *Ecography*, **38**, 130-139.

470 Bartomeus, I., Bosch, J. & Vila, M. (2008) High invasive pollen transfer, yet low deposition on
471 native stigmas in a *Carpobrotus*-invaded community. *Annals of Botany*, **102**, 417-424.

472 Barton, K. (2013) *MuMIn: multi-model inference*. R package version 1.15.1. Available at:
473 <https://cran.r-project.org/web/packages/MuMIn/index.html> (Accessed July 2015).

474 Bascompte, J. (2003) The nested assembly of plant-animal mutualistic networks.
475 *Proceedings of the National Academy of Sciences of the United States of America*,
476 **100**, 9383-9387.

477 Bascompte, J. & Jordano, P. (2007) Plant-animal mutualistic networks: The architecture of
 478 biodiversity. *Annual Review of Ecology Evolution and Systematics*, **38**, 567-593.

479 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *lme4: Linear mixed-effects models*
 480 *using Eigen and S4*. R package version 1.1-10. Available at: [http://CRAN.R-](http://CRAN.R-project.org/package=lme4)
 481 [project.org/ package=lme4](http://CRAN.R-project.org/package=lme4) (Accessed February 2016).

482 Brosi, B. J., and H. M. Briggs. 2013. Single pollinator species losses reduce floral fidelity and
 483 plant reproductive function. *Proceedings of the National Academy of Sciences of the*
 484 *United States of America*, **110**, 13044-13048.

485 Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. & Blüthgen, N. (2007) Specialization,
 486 constraints, and conflicting interests in mutualistic networks. *Current Biology*, **17**,
 487 341-346.

488 Carpintero, S., Reyes-Lopez, J. & De Reyna, L.A. (2005) Impact of Argentine ants
 489 (*Linepithema humile*) on an arboreal ant community in Doñana National Park, Spain.
 490 *Biodiversity and Conservation*, **14**, 151-163.

491 Carvalheiro, L.G., Biesmeijer, J.C., Benadi, G., Fruend, J., Stang, M., Bartomeus, I., Kaiser-
 492 Bunbury, C.N., Baude, M., Gomes, S.I.F., Merckx, V., Baldock, K.C.R., Bennett, A.T.D.,
 493 Boada, R., Bommarco, R., Cartar, R., Chacoff, N., Danhardt, J., Dicks, L.V., Dormann,
 494 C.F., Ekroos, J., Henson, K.S.E., Holzschuh, A., Junker, R.R., Lopezaraiza-Mikel, M.,
 495 Memmott, J., Montero-Castano, A., Nelson, I.L., Petanidou, T., Power, E.F., Rundlof,
 496 M., Smith, H.G., Stout, J.C., Temitope, K., Tscharntke, T., Tscheulin, T., Vila, M. &
 497 Kunin, W.E. (2014) The potential for indirect effects between co-flowering plants via
 498 shared pollinators depends on resource abundance, accessibility and relatedness.
 499 *Ecology Letters*, **17**, 1389-1399.

500 Chittka, L. & Schurkens, S. (2001) Successful invasion of a floral market - An exotic Asian
 501 plant has moved in on Europe's river-banks by bribing pollinators. *Nature*, **411**, 653-
 502 653.

503 Crawley, M.J. (2013) *The R Book*, 2 edn. John Wiley & Sons Ltd, Singapore.

504 Dorado, J., Vazquez, D.P., Stevani, E.L. & Chacoff, N.P. (2011) Rareness and specialization in
 505 plant-pollinator networks. *Ecology*, **92**, 19-25.

506 Dormann, C.F., Jochen, F., Blüthgen, N. & Gruber, B. (2009) Indices, graphs and null models:
 507 analyzing bipartite ecological networks. *The Open Ecology Journal*, **2**, 7-24.

508 Dostal, P., Mullerova, J., Pysek, P., Pergl, J. & Klinerova, T. (2013) The impact of an invasive
 509 plant changes over time. *Ecology Letters*, **16**, 1277-84.

510 Doulier, G. & Stouffer, D. (2015) *Fast network modularity and roles computation by*
 511 *simulated annealing*. R package version 0.2.4 Available at: [https://cran.r-](https://cran.r-project.org/web/packages/rnetcarto/index.html)
 512 [project.org/web/packages/rnetcarto/index.html](https://cran.r-project.org/web/packages/rnetcarto/index.html) (Accessed December 2015).

513 Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Food-web structure and network theory:
 514 The role of connectance and size. *Proceedings of the National Academy of Sciences*
 515 *of the United States of America*, **99**, 12917-12922.

516 Efron, B. (1983) Estimating the error rate of a prediction rule - improvement on cross-
 517 validation. *Journal of the American Statistical Association*, **78**, 316-331.

518 Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P., Dalsgaard, B., de Sassi,
 519 C., Galetti, M., Guimarães, P.R., Beatriz Lomascolo, S., Gonzalez, A.M.M., Pizo, M.A.,
 520 Rader, R., Rodrigo, A., Tylianakis, J.M., Vazquez, D.P. & Allesina, S. (2013) The
 521 dimensionality of ecological networks. *Ecology Letters*, **16**, 577-583.

522 Emer, C., Vaughan, I.P., Hiscock, S. & Memmott, J. (2015) The impact of the invasive alien
 523 plant, *Impatiens glandulifera*, on pollen transfer networks. *Plos One*, **10**, e0143532.

524 Fang, Q. & Huang, S.Q. (2013) A directed network analysis of heterospecific pollen transfer
 525 in a biodiverse community. *Ecology*, **94**, 1176-1185.

526 Fort, H., Vazquez, D.P. & Lan, B.L. (2016) Abundance and generalisation in mutualistic
 527 networks: solving the chicken-and-egg dilemma. *Ecology Letters*, **19**, 4-11.

528 Freeman, L.C. (1979) Centrality in social networks conceptual clarification. *Social Networks*,
 529 **1**, 215-239.

530 Garcia, D., Martinez, D., Stouffer, D.B. & Tylianakis, J.M. (2014) Exotic birds increase
 531 generalization and compensate for native bird decline in plant-frugivore
 532 assemblages. *Journal of Animal Ecology*, **83**, 1441-1450.

533 Gilljam, D., Curtsdotter, A. & Ebenman, B. (2015) Adaptive rewiring aggravates the effects of
 534 species loss in ecosystems. *Nature Communications*, **6**, 10.

535 Gómez, J.M., Verdu, M. & Perfectti, F. (2010) Ecological interactions are evolutionarily
 536 conserved across the entire tree of life. *Nature*, **465**, 918-21.

537 Guimera, R. & Amaral, L.A.N. (2005) Cartography of complex networks: modules and
 538 universal roles. *Journal of Statistical Mechanics: Theory and Experiment*, **PO2001**.

539 <http://archive.mpi.govt.nz/applications/ppin>. *The Plant Pest Information Network (PPIN)*.
 540 Accessed July 2014.

541 <http://www.nonnativespecies.org>. *The Non-native Species Secretariat (NNSS)*. Accessed July
 542 2014.

543 <http://www.europe-aliens.org/>. *Delivering alien invasive species inventories for Europe*
 544 *(DAISIE)*. Accessed July 2014.

545 <http://www.gisin.org>. *Global Invasive Species Information Network (GISIN)*. Accessed July
546 2014.

547 <http://www.issg.org/database/welcome/>. *The Global Invasive Species Database (GISD)*.
548 Accessed July 2014.

549 <http://www.bugwood.org/>. *Center for Invasive Species & Ecosystem Health*. Accessed July
550 2014.

551 <http://www.environment.gov.au/biodiversity/invasive/weeds/>. *Weeds in Australia*.
552 Accessed July 2014.

553 <https://www.nies.go.jp>. *Invasive species of Japan*. Accessed July 2014.

554 Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R.,
555 Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson,
556 E.W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems:
557 theoretical and management aspects of the new ecological world order. *Global*
558 *Ecology and Biogeography*, **15**, 1-7.

559 Huang, Z.-H., H.-L. Liu, and S.-Q. Huang. (2015) Interspecific pollen transfer between two
560 coflowering species was minimized by bumblebee fidelity and differential pollen
561 placement on the bumblebee body. *Journal of Plant Ecology* **8**, 109-115.

562 Hulme, P.E. (2012) Weed risk assessment: a way forward or a waste of time? *Journal of Applied*
563 *Ecology*, **49**, 10-19.

564 Jordano, P., Bascompte, J. & Olesen, J.M. (2003) Invariant properties in coevolutionary
565 networks of plant-animal interactions. *Ecology Letters*, **6**, 69-81.

566 Kaiser-Bunbury, C.N., Valentin, T., Mougai, J., Matatiken, D. & Ghazoul, J. (2011) The
567 tolerance of island plant-pollinator networks to alien plants. *Journal of Ecology*, **99**,
568 202-213.

569 Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R. & Memmott, J. (2007) The impact of an
570 alien plant on a native plant-pollinator network: an experimental approach. *Ecology*
571 *Letters*, **10**, 539-550.

572 Madjidian, J.A., Morales, C.L. & Smith, H.G. (2008) Displacement of a native by an alien
573 bumblebee: lower pollinator efficiency overcome by overwhelmingly higher
574 visitation frequency. *Oecologia*, **156**, 835-845.

575 Martín Gonzalez, A.M., Dalsgaard, B. & Olesen, J.M. (2010) Centrality measures and the
576 importance of generalist species in pollination networks. *Ecological Complexity*, **7**,
577 36-43.

578 Maruyama, P.K., Vizentin-Bugoni, J., Sonne, J., Martín Gonzalez, A.M., Schleuning, M.,
579 Araujo, A.C, Baquero, A.C., Cardona, J., Cotton, P.A., Kohler, G., Lara, C., Malucelli, T.,
580 Marín-Gómez, O.H., Ollerton, J., Rui, A.M., Timmermann, A., Varassin, I.G., Zanata,
581 T.B., Rahbek, C., Sazima, M. & Dalsgaard, B. (2016) The integration of alien plants in
582 mutualistic plant-hummingbird networks across the Americas: the importance of
583 species traits and insularity. *Diversity and Distributions*, 1-10.

584 Memmott, J. & Waser, N.M. (2002) Integration of alien plants into a native flower-pollinator
585 visitation web. *Proceedings of the Royal Society of London Series B-Biological*
586 *Sciences*, **269**, 2395-2399.

587 Montgomery, B.R. & Rathcke, B.J. (2012) Effects of floral restrictiveness and stigma size on
588 heterospecific pollen receipt in a prairie community. *Oecologia*, **168**, 449-458.

589 Morales, C.L. & Traveset, A. (2008) Interspecific pollen transfer: Magnitude, prevalence and
 590 consequences for plant fitness. *Critical Reviews in Plant Sciences*, **27**, 221-238.

591 Moran, M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies.
 592 *Oikos*, **100**, 403-405.

593 Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R² from
 594 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133-
 595 142.

596 Olesen, J.M. & Jordano, P. (2002) Geographic patterns in plant-pollinator mutualistic
 597 networks. *Ecology*, **83**, 2416-2424.

598 Olesen, J.M., Eklundsen, L.I. & Venkatasamy, S. (2002) Invasion of pollination networks on
 599 oceanic islands: importance of invader complexes and endemic super generalists.
 600 *Diversity and Distributions*, **8**, 181-192.

601 Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007) The modularity of pollination
 602 networks. *Proceedings of the National Academy of Sciences of the United States of*
 603 *America*, **104**, 19891-19896.

604 Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2011)
 605 Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society*
 606 *B-Biological Sciences*, **278**, 725-732.

607 Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by
 608 animals? *Oikos*, **120**, 321-326.

609 Ortega, R. (2014) *Web of life*. Available at: <http://www.web-of-life.es> (accessed July 2014).

610 Pysek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants:
 611 Where do we stand? In: *Ecological Studies* eds. M.M. Caldwell, D. Diaz, G. Heldmaier,

612 R.B. Jackson, O.L. Lange, D.F. Levia, H.A. Mooney, E.D. Schulze and U. Sommer), pp.
613 97-125. Springer

614 R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation
615 for Statistical Computing, Vienna, Austria. Available at: [http:// www.R-project.org](http://www.R-project.org)
616 (accessed April 2016).

617 Rezende, E.L., Lavabre, J.E., Guimarães Jr, P.R., Jordano, P. & Bascompte, J. (2007) Non-
618 random coextinctions in phylogenetically structured mutualistic networks. *Nature*,
619 **448**, 925-U6.

620 Richardson, D.M. & Pysek, P. (2006) Plant invasions: merging the concepts of species
621 invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409-
622 431.

623 Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J. & Martinez, N.D. (2009)
624 Predicting invasion success in complex ecological networks. *Philosophical*
625 *Transactions of the Royal Society B-Biological Sciences*, **364**, 1743-1754.

626 Roy, H.E., Adriaens, T., Isaac, N.J.B., Kenis, M., Onkelinx, T., San Martin, G., Brown, P.M.J.,
627 Hautier, L., Poland, R., Roy, D.B., Comont, R., Eschen, R., Frost, R., Zindel, R., Van
628 Vlaenderen, J., Nedved, O., Ravn, H.P., Gregoire, J.-C., de Biseau, J.-C. & Maes, D.
629 (2012) Invasive alien predator causes rapid declines of native European ladybirds.
630 *Diversity and Distributions*, **18**, 717-725.

631 Santos, G.M.d.M., Aguiar, C.M.L., Genini, J., Martins, C.F., Zanella, F.C.V. & Mello, M.A.R.
632 (2012) Invasive Africanized honeybees change the structure of native pollination
633 networks in Brazil. *Biological Invasions*, **14**, 2369-2378.

634 Schleuning, M., Frund, J., Klein, A.M., Abrahamczyk, S., Alarcon, R., Albrecht, M., Andersson,
635 G.K.S., Bazarian, S., Bohning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M.,

- Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H.,
Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.C., Tscharntke, T., Watts, S.,
Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F. & Bluthgen, N.
(2012) Specialization of Mutualistic Interaction Networks Decreases toward Tropical
Latitudes. *Current Biology*, **22**, 1925-1931.
- Solé, R.V. & Montoya, J.M. (2001) Complexity and fragility in ecological networks.
Proceedings of the Royal Society B-Biological Sciences, **268**, 2039-2045.
- Staniczenko, P.P.A., Kopp, J. & Allesina, S. (2013) The ghost of nestedness in ecological
networks. *Nature Communications*, **4**:1391.
- Staniczenko, P.P.A., Lewis, O.T., Jones, N.S. & Reed-Tsochas, F. (2010) Structural dynamics
and robustness of food webs. *Ecology Letters*, **13**, 891-899.
- Stouffer, D.B., Cirtwill, A.R. & Bascompte, J. (2014) How exotic plants integrate into
pollination networks. *Journal of Ecology*, **102**, 1442-1450.
- Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012) Evolutionary conservation
of species' roles in food webs. *Science*, **335**, 1489-1492.
- Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005)
Niche-based modeling as a tool for predicting the risk of alien plant invasions at a
global scale. *Global Change Biology*, **11**, 2234-2250.
- Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant
reproductive mutualisms. *Trends in Ecology & Evolution*, **21**, 208-216.
- Traveset, A. & Richardson, D.M. (2014) Mutualistic interactions and biological invasions.
Annual Review of Ecology, Evolution, and Systematics, **45**, 89-113.
- Traveset, A., Heleno, R., Chamorro, S., Vargas, P., McMullen, C.K., Castro-Urgal, R., Nogales,
M., Herrera, H.W. & Olesen, J.M. (2013) Invaders of pollination networks in the

Galapagos Islands: emergence of novel communities. *Proceedings of the Royal Society B-Biological Sciences*, **280**, 20123040.

Trøjelsgaard, K., Jordano, P., Carstensen, D.W. & Olesen, J.M. (2015) Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. *Proceedings of the Royal Society B-Biological Sciences*, **282**, 20142925.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351-1363.

Warton, D.I. & Hui, F.K.C. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, **92**, 3-10.

Waser, N.M. & Ollerton, J. (2006) *Plant-Pollinator Interactions: From Specialization to Generalization*, 1th edn. University of Chicago Press, Chicago.

Willmer, P. G., and K. Finlayson. 2014. Big bees do a better job: intraspecific size variation influences pollination effectiveness. *Journal of Pollination Ecology*, **14**, 244-254.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*, 1th edn. Springer, New York.

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676

677 **SUPPORTING INFORMATION**

678 Additional Supporting Information can be found in the online version of this article:

679

680 **APPENDIX S1.** Outlier detection analyses.

681 **TABLE S1** – Description of the networks used for the analyses of the species’ roles of plants
682 and pollinators in the alien and native range.

683 **TABLE S2.** List of the target species and the networks in which they were recorded. Network
684 ID follows Figure 1 and Table S1 in which details of each network are provided.

685 **TABLE S3.** Results of the Linear Mixed-Effect Models (LMMs) and the Linear Regression
686 Models (LMs) testing whether latitude and trophic level interact with species range to
687 determine species’ roles.

688 **TABLE S4.** Species roles on pollination networks following Olesen et al. (2007): Peripheral $z \leq$
689 2.5, $c \leq 0.62$; Connector $z \leq 2.5$, $c > 0.62$; Module hub $z > 2.5$, $c \leq 0.62$; Network hub $z > 2.5$, c
690 > 0.62 . The first number is the number of occurrences in networks in the species native
691 range, and the second number is the species occurrences in networks in its alien range.

692 **TABLE S5.** Correlation between normalised degree, closeness, betweenness, c and z scores
693 measured with (a) individual entries, i.e. the value of the role of each species in each
694 network is taking into account, as used in the Linear Mixed Models, and (b) when the
695 averages for each species are considered, as used in the Linear Regressions of the
696 manuscript. Values correspond to the Spearman correlation coefficient ρ .

697

698

699 **BIOSKETCHES**

700 **Carine Emer** is a community ecologist interested on understanding how anthropogenic
701 disturbance affect animal-plant interactions. Her research includes both mutualistic and

702 antagonistic processes in tropical and temperate habitats. Recently she has studied the
703 effects of invasive species, habitat loss and fragmentation on ecological networks. She is
704 currently a postdoctoral researcher at the Universidade Estadual Paulista (UNESP) in Brazil.
705 The authors are part of a collaboration established during her doctorate at the University of
706 Bristol, UK.

707 **Authors contributions:** CE and JMT developed the study framework. CE gathered the data,
708 ran the analyses, and wrote the manuscript. IPV provided statistical advice. DM contributed
709 with the study design and discussion. JM advised on the collection of the field data, and JM
710 and JMT commented and edited the versions of the manuscript.

711

712 **TABLES AND FIGURES LEGEND**

713

714 **Table 1.** The 17 plant and pollinator species analysed in this study (see Table S1 for further
715 information about each network).

716 **Table 2.** Results of the Linear Mixed-Effects Models (LMMs) testing whether species roles
717 differ from the native to the alien range. Pseudo R-squared values were calculated to
718 estimate the variance explained by the fixed and random structure of each model: $R^2_{\text{fix+rand}}$ -
719 estimates total variance explained by the fixed and random effects combined; R^2_{fix} -
720 estimates the variance explained by range; R^2_{rand} estimates the contribution of the random
721 effects only.

722 **Figure 1.** The location of the 48 plant-pollinator networks. Panels A-G show the location of
723 those networks that overlap in the full map. Numbers are the individual codes of each
724 network identity (see Supplementary Material).

725 **Figure 2.** Results of the linear regression models testing whether a species' role in the native
726 range predicts its role in the alien range. (a) Normalised degree; (b) Closeness; (c)
727 Betweenness; (d) c-score; and (e) z-score. Results of normalised degree are shown after the
728 removal of an outlier.

729 **Table 1**

Plant species	Family	Number of networks present	
		Native networks	Alien networks
<i>Achillea millefolium</i> L.	Asteraceae	4	5
<i>Cirsium arvense</i> (L.) Scop	Asteraceae	3	6
<i>Cytisus scoparius</i> (L.) Link	Fabaceae	1	1
<i>Eupatorium cannabinum</i> L.	Asteraceae	1	2
<i>Hieracium pillosela</i> L.	Asteraceae	2	4
<i>Hypochaeris radicata</i> L.	Asteraceae	5	6
<i>Leucanthemum vulgare</i> Lam.	Asteraceae	2	4
<i>Lotus corniculatus</i> L.	Fabaceae	3	1
<i>Taraxacum officinale</i> F.H. Wigg	Asteraceae	4	1
<i>Trifolium pratense</i> L.	Fabaceae	2	4
<i>Trifolium repens</i> L.	Fabaceae	3	10
<i>Verbascum thapsus</i> L.	Scrophulariaceae	2	3
Total plants` occurrences		31	47
Insect species	Order		
<i>Apis mellifera</i> L.	Hymenoptera	9	28
<i>Bombus hortorum</i> L.	Hymenoptera	7	4
<i>Bombus terrestris</i> L.	Hymenoptera	9	6
<i>Eristalis tenax</i> L.	Diptera	5	11
<i>Pieris rapae</i> L.	Lepidoptera	3	6
Total insects` occurrences		33	46
Total		64	102

730 **Table 2**

Linear Mixed-Effects Models						
	Est	t	p	R ² _{fix-rand}	R ² _{fix}	R ² _{rand}
Normalised degree	0.305	1.227	0.226	0.408	0.011	0.397
Closeness	-0.108	-1.188	0.237	0.939	0.003	0.936
Betweenness	0.116	0.326	0.747	0.201	0.000	0.201
z – score	-0.029	-0.158	0.875	0.285	0.000	0.285
c - score	0.028	1.076	0.285	0.378	0.010	0.377

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